

Description of a new beetle-like psocid (Insecta: Psocoptera: Protractopsocidae) from Turkey showing an unusual sexual dimorphism

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Description of a new beetle-like psocid (Insecta: Psocoptera: Protractopsocidae) from Turkey showing an unusual sexual dimorphism. - *Reticulopsocus besucheti* gen. n., sp. n. is described and illustrated from a series of specimens of both sexes collected under stones in southern Turkey. The new genus is closely related to the Mediterranean genera *Chelyopsocus* Lienhard and *Philedaphia* Lienhard. Some illustrations of the type genus of the family, *Protractopsocus* Mockford, are also provided. Both sexes of the new genus are elytropterous and beetle-like in habitus but the fore wing venation is strongly sexually dimorphic: males have a normal venation, though somewhat simplified, females however, have a highly apomorphic, reticulate venational pattern. A key to the genera of the family Protractopsocidae is provided.

Keywords: *Reticulopsocus* - *Protractopsocus* - *Chelyopsocus* - *Philedaphia* - new genus - new species - wing venation - elytroptery - soil fauna - Mexico.

INTRODUCTION

Sometimes spectacular discoveries within a particular insect group are not due to the targeted collecting of a specialist but to the quick-witted reaction of a non-specialist encountering an unusual representative of a group, which he did not really search for. So it is not surprising that litter-dwelling beetle-like psocids are more effectively collected by coleopterists interested in soil-fauna than by psocidologists. This is the case in the Oriental genus *Coleotroctellus* Lienhard, 1988 (Electrentomoidea: Troctopsocidae) where three of the four known species have been discovered by entomologists searching for soil Coleoptera by sifting plant debris in forests. *C. burckhardti* and *C. loebli* were collected by my Swiss colleagues Daniel Burckhardt and Ivan Löbl, *C. venosus* by the Russian coleopterist Sergei Kurbatov.

A similar and very recent collecting success is due to my colleague Claude Besuchet, well known specialist of pselaphine Coleoptera and former curator at the Natural History Museum of Geneva. When turning stones in a pine forest in southern Turkey in May 2004, he immediately recognized some fast-moving dark brown "peculiar beetles" on the undersurfaces of the stones and identified them as unusual

psocids. Remembering my interest in these insects, he made a special effort to collect a representative series of these intriguing creatures. Back to Geneva he immediately gave them to me, commenting that he had apparently found two kinds (two species?) of very particular psocids, both of them with dark brown elytriform fore wings, one of them with a characteristically reticulate structure, the other with a relatively simple venation.

What he initially thought to be two different species are actually males and females of a new electrentomoid psocid exhibiting one of the most intriguing cases of sexual dimorphism ever observed in the order Psocoptera. This species is here considered as a representative of a new genus of the family Protroctopsocidae Smithers, which is already represented in the Mediterranean region by the genera *Chelyopsocus* Lienhard and *Philedaphia* Lienhard.

Mockford (1967) described the very particular monotypic Mexican genus *Protroctopsocus* in the family Troctopsocidae. Smithers (1972: 338) later placed *Protroctopsocus* Mockford in a subfamily of its own: Protroctopsocinae Smithers. Based on the short phylogenetic discussion presented by Lienhard (1995), two other troctopsocid genera, *Chelyopsocus* Lienhard and *Philedaphia* Lienhard, have been assigned to this subfamily by Lienhard & Mockford (1997). Subsequently elevated to family rank, this taxon has been assigned to the superfamily Electrentomoidea Enderlein (see Enderlein, 1911) (suborder Troctomorpha, infraorder Amphientometae) by Lienhard & Smithers (2002).

The superfamily Electrentomoidea sensu Lienhard & Smithers (2002) contains four relatively small families comprising 20 genera, most of them monotypic (12 genera), the others containing only few species (6 genera with 2-5 spp., 2 with 7-8 spp.) (see Lienhard & Smithers, 2002 and Lienhard, 2003). All genera are characterized by striking autapomorphies but their relationships are still poorly understood (see Lienhard & Mockford, 1997). It is not the purpose of this paper to analyse these relationships but to introduce a new species representing a new genus and to present some morphological characters, which could be of phylogenetic significance for future analyses. A sample of the new species has also been sent to Kazunori Yoshizawa for DNA extraction (see "Material and Methods").

The family Protroctopsocidae is characterized by the following synapomorphies of its genera: presence of larval glandular hairs on thorax and abdomen (at present only confirmed in *Protroctopsocus* and *Philedaphia*, see Lienhard, 1995; nymphs of other genera not known); AP joined to vein *m*; endophallus with a conspicuous eversible pouch, sac-shaped (Figs 10, 11, 29) or tube-shaped (Lienhard, 1995: fig. 24) when everted and characteristically folded in resting position (Fig. 9 and Lienhard, 1995: fig. 23 and Garcia Aldrete, 1982: fig. 10) (this character not confirmed in *Chelyopsocus*, the male of which is not known).

The main diagnostic characters of protoctopsocid genera are mentioned in the key below. At present the following four genera and five species are known:

Protroctopsocus Mockford, 1967: *P. enigmaticus* Mockford, 1967 (Mexico), ♂ ♀. - See Mockford (1967) and Garcia Aldrete (1982).

Chelyopsocus Lienhard, 1980: *C. garganicus* Lienhard, 1980 (Italy), ♀ (♂ unknown). - See Lienhard (1980, 1998).

Philedaphia Lienhard, 1995: *P. aphrodite* Lienhard, 1995, type species (Cyprus), ♂ ♀. - *P. hauseri* (Lienhard, 1988) (Greece), ♀ (male unknown, parthenogenetic). - See Lienhard (1988, 1995, 1998).

Reticulopsocus gen. n.: *R. besucheti* sp. n. (Turkey), ♂ ♀. - See description below.

MATERIAL AND METHODS

The following protoctopsocids have been examined for this study:

Reticulopsocus besucheti gen. n., sp. n.: type material (MHNG), see description below. NOTE. Thorax (except fore wings) and basal half of abdomen of one paratype male (MHNG 7625) were sent to Kazunori Yoshizawa (SEHU) for DNA extraction in June 2004; after their return, the exoskeleton of these parts was mounted on a permanent slide together with the other parts of the specimen.

Chelyopsocus gargaricus Lienhard: type material (2 ♀, MHNG), see Lienhard (1980).

Philedaphia aphrodite Lienhard: type material (♂♂ and ♀♀, MHNG), see Lienhard (1995).

Philedaphia hauseri (Lienhard): type material (♀♀, MHNG), see Lienhard (1988).

Protoctopsocus enigmaticus Mockford: 1♂, 1♀ (both slightly brachypterous, with elytriform fore wings) (MHNG), MEXICO: Mexico, K. 87, Toluca - Tejupilco, 1750m, 4.VI.1988, leg. A. Cadena, L. Cervantes.

Habitus photographs were made with the AutoMontage® system using a JVC® video camera mounted on a Leica MZ APO stereomicroscope and slightly reworked with ADOBE Photoshop®.

Abbreviations used in the descriptions: A = antenna length; AP = areola postica (cubital loop in fore wing); BL = body length (in alcohol); f1, f2, f3, f4 = length of basal four antennal flagellomeres; F = hind femur length; FW = fore wing length; IO/D = shortest distance between compound eyes divided by antero-posterior diameter of compound eye in dorsal view of head; P4 = fourth (apical) article of maxillary palpus; PS = pterostigma (fore wing); T = hind tibia length; t1, t2, t3 = tarsomeres of hind tarsus (lengths measured from condyle to condyle). For standard abbreviations concerning wing venation, see Lienhard (1998).

Other abbreviations: BISU = Biological Sciences, Illinois State University, Normal; MHNG = Muséum d'histoire naturelle de la Ville de Genève, Switzerland; SEHU = Systematic Entomology, Hokkaido University, Sapporo; UNAM = Universidad Nacional Autónoma de México.

DESCRIPTION AND DISCUSSION

Reticulopsocus gen. n.

Diagnosis (see also key to the genera of Protoctopsocidae below). Brachypterous and flightless, general habitus somewhat beetle-like (Pl. 1AB) due to blackish brown elytriform fore wings with thickened veins; venation slightly simplified in male, forming a highly apomorphic, reticulate pattern in female. Hind wings strongly

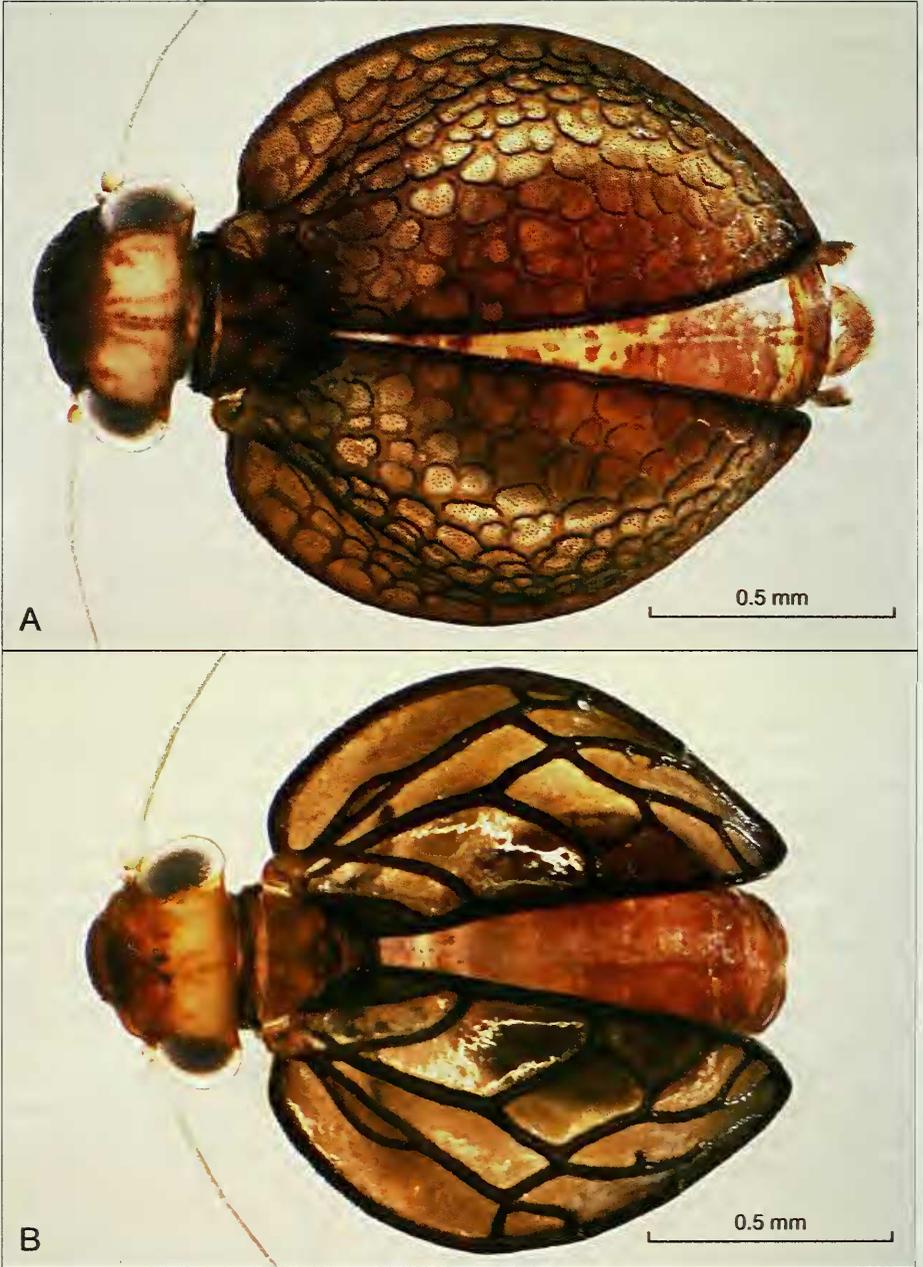


PLATE 1

Reticulopsocus besucheti gen. n., sp. n., habitus in alcohol, dorsal view, legs not visible on photograph. A: female paratype. B: male holotype [epiproct and paraprocts not visible, they were hidden by the extruded phallic structures (cf. Figs 10, 11) that have been deleted from the photograph].

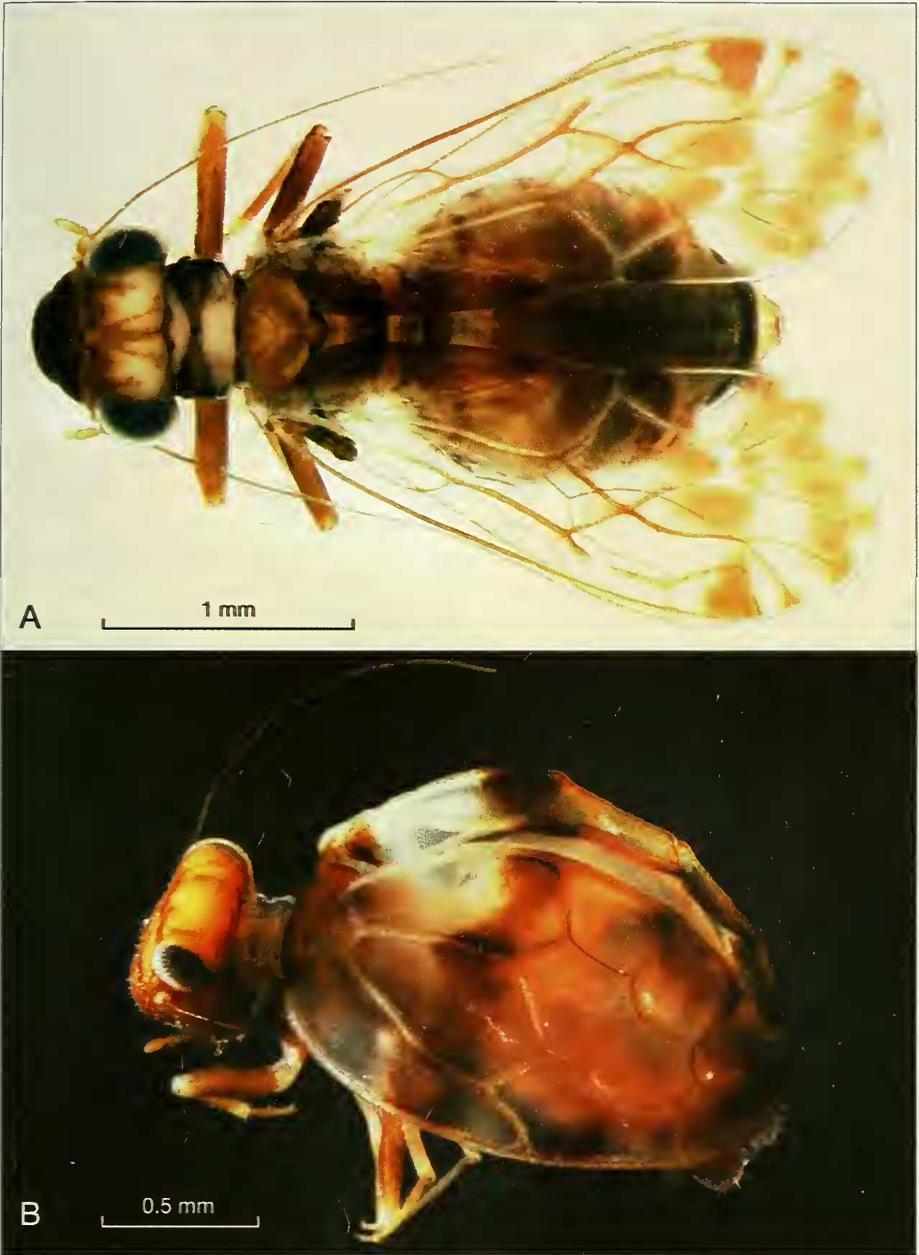


PLATE 2

Habitus, in alcohol. A: *Philedaphia aphrodite* Lienhard, female paratype (dorsal view). B: *Chelyopsocus garganicus* Lienhard, female paratype (dorso-lateral view; with right/left reversal of photograph for publication; left wing of the same specimen illustrated in Lienhard, 1998: pl. 9g).

reduced, veinless (Fig. 3). Antenna 14-segmented. Frons about equal in length to post-clypeus in anterior view. Ocelli present in male, close to each other, absent in female. Outer cusp of lacinial tip distinctly bidentate (Fig. 19), incisive region of mandibles acute (Fig. 21). Fore femur with a longitudinal ventral row of particularly well-developed sculptural denticles on anterior side (Fig. 22). Pretarsal claw with one preapical denticle and some ventral and lateral microtrichia (Fig. 23). Principal veins of fore wing not clearly recognizable in female (Pl. 1A, Fig. 1). Venation of male fore wing (Pl. 1B, Figs 4-6) similar to that of other genera of the family, but slightly simplified and somewhat variable; membrane of wing cells slightly concave.

Epipect and paraproct (Figs 8, 14) with some simple stout marginal setae in both sexes, setae on weakly differentiated sense cushion of paraproct without basal rosettes. Lateral hind margin of male clunium simple, roughly right-angled, without densely pilose posterior lobe (Fig. 8). Hypandrium simple (Fig. 7). Phallosome V-shaped (Figs 9, 11), lacking medio-apical sclerite; lateral struts simple but curved to the middle at their apex; latero-apical sclerites elongated, articulated to the apical angle of lateral struts close to a pore-bearing membranous zone. Endophallic pouch sac-shaped in everted position (Fig. 10), centro-ventral pore-bearing lobe of endophallus apically bilobed, its position varying according to the degree of eversion of the endophallic sac (cf. Figs 9, 11). Female subgenital plate (Fig. 12) with 2 stout apical setae and with sclerotized latero-dorsal zones on margin, these joined to T-shaped sclerite by small sclerotized bridges. External valve of gonapophyses (Fig. 13) deeply bilobed. Spermathecal duct (Figs 15, 16) relatively short, straight and of same width throughout its length; spermatheca situated on a slightly sclerotized oval zone surrounded by fine wrinkles; spermathecal sac with a distinct basal zone bearing a field of inward-directed papillae near opening of duct; wall of spermathecal sac loosely covered with small pores each bearing a short outward-directed microtubular appendix (Fig. 17).

Type species. *Reticulopsocus besucheti* sp. n.

Etymology. The genus name is of masculine gender and refers to the reticulate venational pattern of female fore wing.

Remarks. See discussion of the type species.

Reticulopsocus besucheti sp. n.

Figs 1-23, Pl. 1

MATERIAL

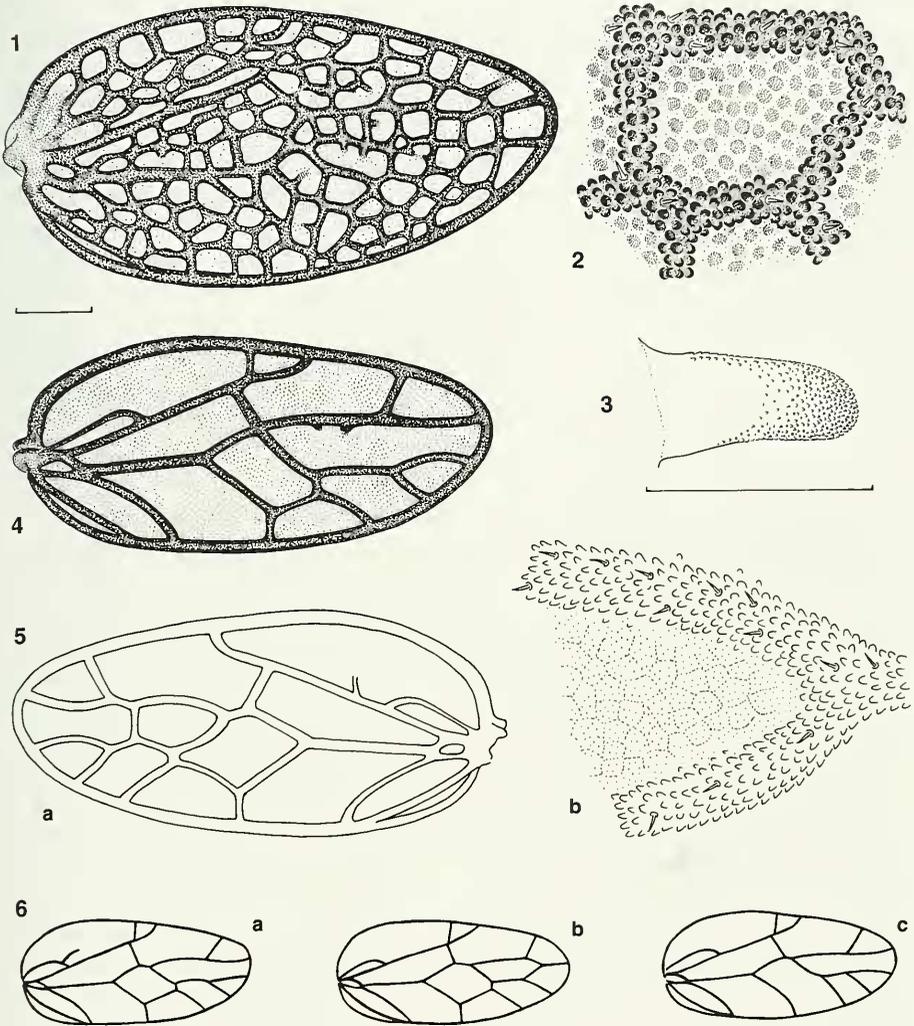
Holotype ♂. TURKEY (Mersin Province): Toros mountains, valley from Mersin town up to village Arslanköy, close to village Aladag, 850 m, forest of *Pinus* sp., under stones, 2.V.2004, leg. C. Besuchet (no. 34); the specimen has been dissected and mounted on two slides (MHNG 7645). Allotype ♀, same data as for holotype; dissected and mounted on two slides (MHNG 7646). Other paratypes: 4♂, 5♀, same data as for holotype.

ETYMOLOGY

The species is dedicated to Dr Claude Besuchet who collected the type material (see also "Introduction").

DESCRIPTION

MALE. *Coloration.* See Pl. 1B. Body generally medium to dark brown, vertex light brown with some darker spots. Compound eye uniformly dark brown (observed after some months in alcohol). Antenna and maxillary palpus light brown; legs light to



FIGS 1-6

Reticulopsocus besucheti gen. n., sp. n.: 1, right fore wing (♀ allotype); 2, idem, detail of wing sculpture (in apical half of wing); 3, hind wing (♀ allotype, coloration not shown); 4, right fore wing (♂ holotype); 5, left fore wing (♂ paratype MHNG 7625), venation (5a) and detail of sculpture (5b) in centre of wing (coloration not shown); 6a-c, schematic presentation of variability of male fore wing venation (see text). Scale bars: 0.2 mm (Figs 1, 4, 5a; 3).

medium brown, with dark brown coxae and femora. Membrane of fore wing uniformly dark brown, glossy, veins blackish brown. Abdomen with dense red-brown hypodermal pigmentation on dorsal and ventral side, terminalia brown.

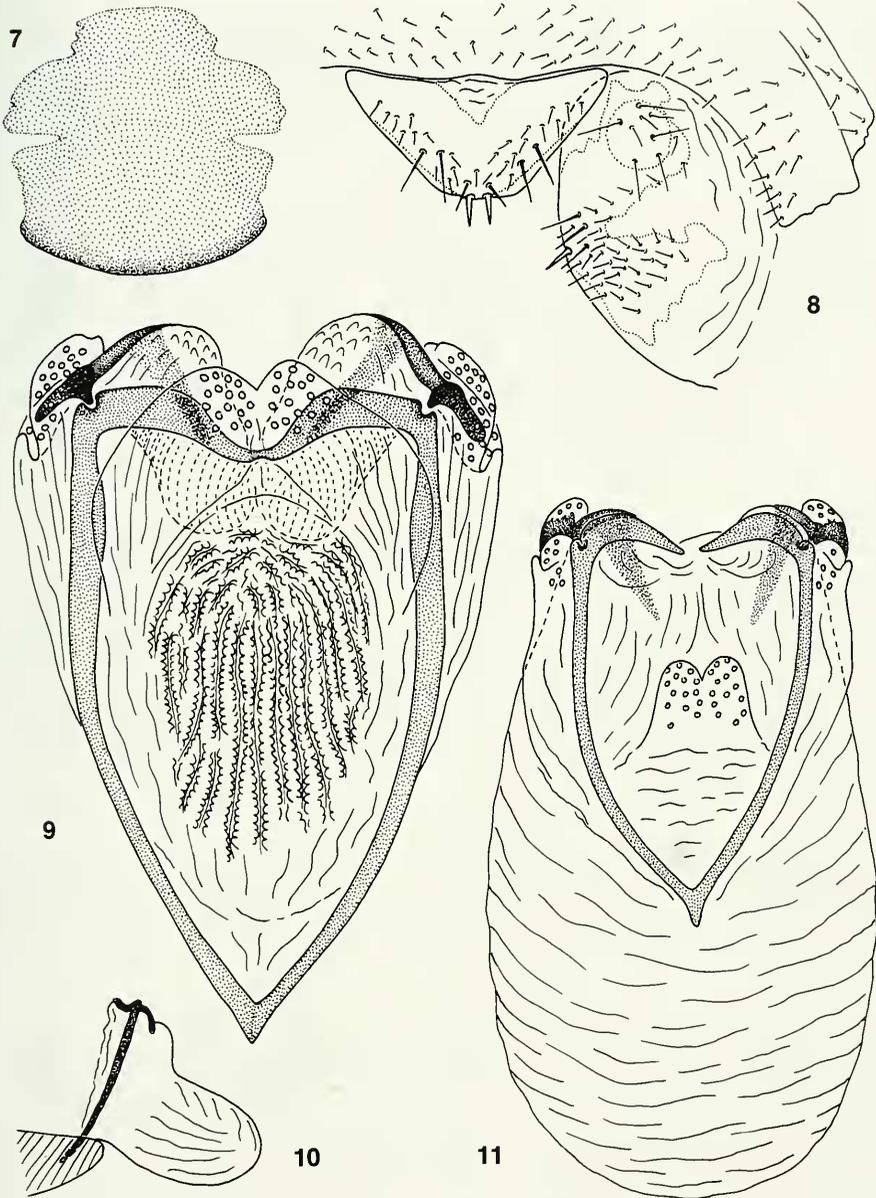
Morphology. See generic diagnosis, with the following complements. Vertex antero-posteriorly rounded, outline slightly undulated in frontal view (cf. Garcia Aldrete, 1982: fig. 1), due to the presence of a shallow dimple on each side, about half

way between compound eye and vertical suture; frontal suture also visible. Vertex with distinct tubercular sculpture, locally forming a more or less scale-like pattern, pilosity very short. Antennal flagellomeres with annulate sculpture and relatively long slightly wavy hairs (length several times the width of flagellomere). Maxillary palpus as in Fig. 20; sensilla on distal margin of labrum as in Fig. 18, the placoid sensilla lacking central cones. Internal microtrichial field of galea (mentioned for *Philedaphia* by Lienhard, 1998: fig. 44b) absent or only weakly developed. Prodorsum short, dorsally covered by prominent and almost sharp-edged anterior margin of mesonotum fitting into the occipital margin of the head-capsule (contracted condition of the body). Sculpture of mesonotum similar to that of vertex. Elytriform fore wings in resting position joined along posterior margin to form a hemispherical sclerotized capsule covering the soft abdomen. Veins of fore wing with distinct rounded tubercles, dorsal membrane glossy, only finely granular and locally with fine reticulate pattern (Fig. 5b). Vein *an2* absent. Observed variability of wing venation (often asymmetrical on same individual; totally 9 wings of 5 males examined; right wing of paratype male MHNG 7625 lost during capture): PS basally closed (Fig. 4) in 7 wings, open (Fig. 5a) in 2 wings; rudimentary second section of *sc* present in 3 wings, bifurcating from *r* proximally to *r1-rs* bifurcation (Fig. 5a: 1 wing) or bifurcating from basal section of *sc* near its meeting point with *r* (Fig. 6a: 2 wings); *rs* and *m* basally meeting in a point (Fig. 4) or fused for a short length (Fig. 5a) and in 1 wing distally joined by a crossvein (Fig. 5a: cell R5 subdivided in middle), the latter completely absent (5 wings) or rudimentary (3 wings) (Pl. 1B and Fig. 4); in 1 wing *r4+5* fused to *m1* for the portion before the wing margin, resulting in a closed cell R5 (Fig. 6b); *cu1* (i. e. AP) distally fused to *m3*, resulting in a large AP apparently joined to *m* by a short crossvein and *m* appearing only 2-branched (Figs 4, 5a: 6 wings), or proximal section of *cu1* completely absent, resulting in an apparently 3-branched *m* and absence of AP due to simple vein *cu* (Fig. 6c: 3 wings). Hind wing strongly reduced (cf. Fig. 3) and almost vertically protruding from thorax (transparent through fore wings in Pl. 1B). Pearman-organ of hind coxa incomplete, only tympanum visible, coxal rasp not differentiated; tibiae with two apical spurs; number and position of microtrichia of pretarsal claws somewhat variable, usually three relatively long seta-like ventral microtrichia at base and on ventral edge (cf. Fig. 23). Phallosome in resting position as in Fig. 9, with everted endophallic sac as in Fig. 11, hook-shaped lateral struts medially separated (Fig. 11) or joined by a small sclerotized bridge (Fig. 9); membrane near apex of latero-apical sclerite on each side with a basally directed, slightly sclerotized longitudinal zone (Figs 9, 11).

Measurements (δ holotype, in μm). BL = 1450; FW = 1280; A = 1510; f1 = 125; f2 = 150; f3 = 155; f4 = 160; F = 365; T = 570; t1 = 285; t2 = 53; t3 = 78; IO/D = 1.5.

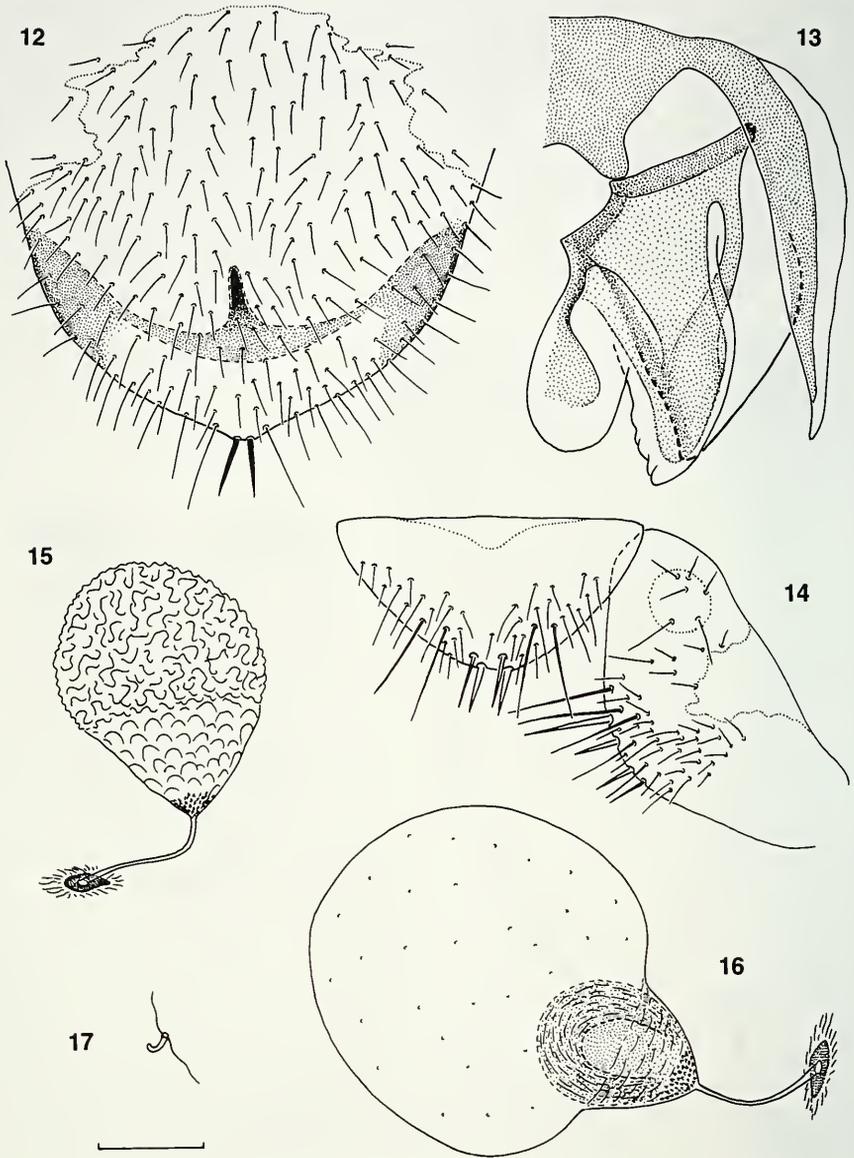
FEMALE. *Coloration.* Same as in male, but membrane of fore wing dull (Pl. 1A).

Morphology. See generic diagnosis and description of male, with the following complements. Sculpture of vertex with large rounded tubercles (their diameter about twice the diameter of the alveoli of the fine hairs on vertex), usually not forming scale-like pattern. Pilosity of antennal flagellum much sparser and shorter than in male.



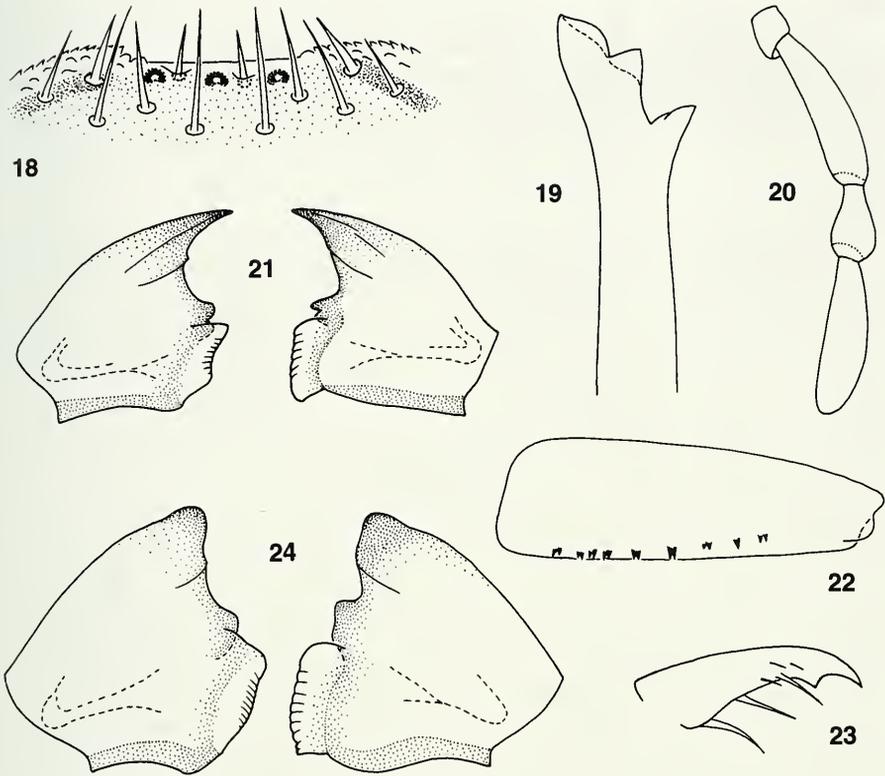
Figs 7-11

Reticulopsocus besucheti gen. n., sp. n., male (paratype MHNG 7625: Figs 7-9, holotype: Figs 10-11): 7, hypandrium (pilosity not shown); 8, epiproct, right paraproct, right angle and hind margin of clunium (coloration not shown, brown cuticular pigmentation of epiproct and paraproct delimited by dotted lines); 9, phallosome (ventral view, endophallic sac not everted); 10, phallosome with everted endophallic sac, in situ (lateral view, schematic, hypandrium hatched); 11, phallosome with everted endophallic sac, slide-mounted (dorsal view, centro-ventral pore-bearing lobe of endophallus visible by transparency, lower magnification than in Fig. 9).



Figs 12-17

Reticulopsocus besucheti gen. n., sp. n., female (allotype: Figs 12-15, paratype MHNG 7648; Figs 16-17): 12, subgenital plate (general coloration of ventral side not shown, brown cuticular pigmentation anteriorly delimited by dotted line); 13, gonapophyses; 14, epiproct and right paraproct (coloration not shown, brown cuticular pigmentation delimited by dotted lines); 15, spermatheca (empty spermatheca of virgin female); 16, spermatheca of mated female, with spermatophore (sperm packet) in basal zone of sac; 17, pore with microtubular appendix of spermathecal membrane (scale bar 0.02 mm).



FIGS 18-24

Figs 18-23. *Reticulopsocus besucheti* gen. n., sp. n., female allotype: 18, sensilla on distal margin of labrum; 19, lacinial tip; 20, maxillary palpus (pilosity not shown); 21, mandibles (anterior view); 22, anterior side of fore femur (base left, apex right; general sculpture not shown); 23, pretarsal claw. - Fig. 24. *Chelyopsocus garganicus* Lienhard, female holotype: mandibles (anterior view, same magnification as Fig. 21).

Principal veins of fore wing not clearly recognizable, except vein *an1* and basal parts of *r* and *m+cu* visible as particularly well-differentiated straight venational structures within the reticulate pattern covering the whole wing (Pl. 1A, Fig. 1) and delimiting small cells of irregular shape, these cells sometimes partially open due to incomplete veins (see Fig. 1). Veins with distinct, rounded tubercles; dorsal membrane slightly rugose and reinforced by sclerotized circular plaques (Fig. 2). Dorsal valve of gonapophyses particularly broad (Fig. 13). The terminalia of two female paratypes have been dissected, one of them (MHNG 7646 allotype) proved to be virgin, its spermatheca being shrivelled and empty (Fig. 15), in the other one (MHNG 7648) a simple spermatophore (sperm packet) could be observed in the basal zone of the spermathecal sac (Fig. 16).

Measurements (♀ allotype, in μm). BL = 1730; FW = 1470; A = 1460; f1 = 120; f2 = 150; f3 = 155; f4 = 170; F = 400; T = 610; t1 = 285; t2 = 55; t3 = 88; IO/D = 1.7.

BIOLOGY

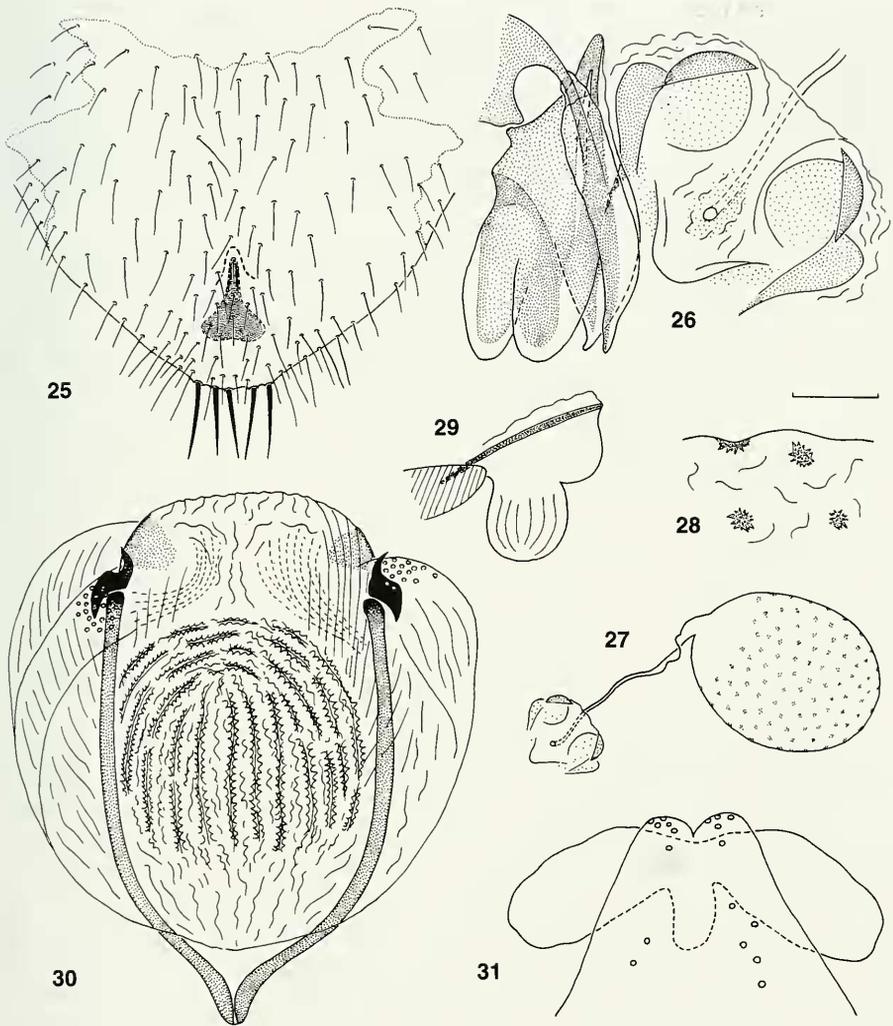
The type series was collected under stones lying on the soil of a relatively open forest of *Pinus* sp., situated in a mountainous region of southern Turkey, about 30 km from the Mediterranean coast. When disturbed, these black, hemispherical, beetle-like insects moved quickly on the underside of the stones (C. Besuchet, pers. comm.).

DISCUSSION

The definition of the family Protoctopsocidae and its generic and specific composition have already been presented in the "Introduction". Within this family the three Mediterranean genera *Philedaphia*, *Chelyopsocus* and *Reticulopsocus* gen. n. undoubtedly form a monophyletic group defined by the following synapomorphies: antenna 14-segmented, female subgenital plate with sclerotized latero-dorsal zones on margin, endophallus with pore-bearing central lobe. Its sister-group is the Mexican genus *Protoctopsocus*, which is characterized by several plesiomorphic features and by the autapomorphic basal enlargement of P4 and the complex sclerotizations around the spermapore (Fig. 26). The three Mediterranean genera can be assigned to two phylogenetic clades, one comprising *Philedaphia*, characterized by the complex phallosome (see key below), and the other comprising *Chelyopsocus* and *Reticulopsocus*. The latter two genera have a very similar spermatheca structure (simple spermapore, membrane of spermathecal sac with pores bearing microtubular appendices; but spermatheca lacking inward-directed basal papillae near opening of duct in *Chelyopsocus*) which can be interpreted as a probable synapomorphy. In both other protoctopsocid genera (i.e. *Protoctopsocus* and *Philedaphia*) the membrane of the spermathecal sac lacks basal papillae and pores with microtubular appendices; however, in *Philedaphia* this membrane bears regularly distributed inward-directed spine-like structures (see Lienhard, 1988: fig. 7 and 1995: fig. 14), which are probably homologous to the inward-directed, small, rugose plates present in *Protoctopsocus* (Figs 27, 28).

Chelyopsocus is characterized by the clearly apomorphic blunt incisive region of the mandibles (Fig. 24; this newly observed character state was confirmed for both specimens known of this genus, holotype and paratype females of *C. garganicus*); in all other protoctopsocid genera this region is acute, corresponding to the plesiomorphic condition within Psocoptera (cf. Fig. 21). The broad and only weakly subdivided outer cusp of the lacinial tip can also be interpreted as an autapomorphy of this genus; all other protoctopsocids show a distinct indentation (cf. Fig. 19).

Occasional brachyptery with a tendency towards elytriform fore wings can be observed in *Protoctopsocus*, but it is without sexual dimorphism. Elytroptery seems to be genetically fixed in the female of *Chelyopsocus* (male not known) and in both sexes of *Reticulopsocus*, where a strong sexual dimorphism occurs. The male exhibits a "moderate elytroptery" (with essentially normal wing venation, similar to that present in the female of *Chelyopsocus* and in the brachypterous morph of *Protoctopsocus*), whereas the female shows a "perfect elytroptery" with densely reticulate fore wings forming a regularly vaulted and uniformly structured, hemispherical covering of the abdomen strongly resembling elytra in Coleoptera.



FIGS 25-31

Figs 25-30. *Proctroctopsocus enigmaticus* Mockford (female: Figs 25-28; male: Figs 29-30): 25, subgenital plate (general coloration of ventral side not shown, brown cuticular pigmentation anteriorly delimited by dotted line); 26, gonapophyses and sclerotizations around spermapore; 27, spermatheca; 28, rugose areas of spermathecal membrane (scale bar 0.02 mm); 29, phallosome with everted endophallic sac, in situ (lateral view, schematic, hypandrium hatched); 30, phallosome (ventral view). - Fig. 31. *Philedaphia aphrodite* Lienhard, male paratype: medio-apical sclerite of phallosome (coloration not shown) and membranous pore-bearing central lobe of endophallus (ventral view, endophallic sac not everted).

The presence of morphologically so different brachypterous morphs within the same species has never been observed before in Psocoptera. In the other electrentomoid genus with beetle-like females, the litter-dwelling *Coleotroctellus* Lienhard (see "Introduction"), males are always macropterous, with normal venation and fully

developed hind wings. In that genus the mobility of the males apparently represents a more important evolutionary advantage than it could be offered by an efficient abdominal protection in both sexes (Lienhard, 2002). In *Reticulopsocus* this is apparently not the case. Males have also become flightless and perhaps they are on the way to evolve towards a “perfect elytroptery” as it has already been genetically fixed in females. The many venational aberrations observed in males (see description) may be interpreted as an indication of a diminishing selection pressure for “normal” venation in these brachypterous and flightless animals.

In *Coleotroctellus* the females show a beetle-like habitus similar to that of the female of *Reticulopsocus*. In both genera shape and length of the dark brown female fore wings are about the same. However, in *Coleotroctellus* the sclerotized vaulted wing membrane is stabilized by a series of thickened longitudinal veins derived from the normal venation of the family Troctopsocidae, which is very similar to the normal venation of Proctroctopsocidae. In some species these veins are relatively easy to homologize with the normal venation (*C. burckhardti* and *C. loebli*, see Lienhard, 1988 and Lienhard & Mockford, 1997), but in *C. venosus* the multiplication of longitudinal veins makes this homologization very difficult. *C. venosus* apparently is the most derived form resulting from an evolutionary trend towards “perfect elytroptery”, where the vaulted fore wing membrane is mechanically stabilized by numerous parallel longitudinal ribs (see Lienhard & Mockford, 1997: figs 8-10). As we have seen above, another type of “perfect elytroptery” has evolved in *Reticulopsocus*, based on a different constructional principle, which consists of “wire-netting” the vaulted fore wing membrane by a dense reticulate venational pattern (Pl. 1A and Fig. 1).

Reticulate fore wings are very rare in Psocoptera. Some distinct but very fine reticulate sculpture can be observed in the strongly reduced scale-like fore wings of *Lepinotus reticulatus* Enderlein (Trogidae, suborder Trogiomorpha) and in the parchment-like elytriform fore wings of *Badonnelia titei* Pearman (Sphaeropsocidae, suborder Troctomorpha) (*L. reticulatus*: see Lienhard, 1998: fig. 26d; *B. titei*: see Pearman, 1958: fig. 6, New, 1974: fig. 130, Lienhard, 1982: fig. 3). But in these cases the reticulation is not directly derived from the wing venation. The only family, where extensive venational reticulation in fore wings is currently known are the Calopsocidae (suborder Psocomorpha; see Thornton & Smithers, 1984). In some species the reticulate venation is especially well-developed in the apical half of the wing, but species with almost completely reticulate wings are also known (e. g., *Calopsocus reticuloides* Thornton & Smithers). In Calopsocidae this reticulate condition is usually also combined with some wing shortening and a slight tendency towards elytroptery, but hind wings are always well-developed, with normal venation, and probably these psocids are all able to fly. Sexual dimorphism in wing structure is not known in Calopsocidae (see male and female of *C. reticuloides*, Thornton & Smithers, 1984: figs 116 and 121). Calopsocids usually live on vegetation and with a fore wing length of several millimeters they are all much larger than *Reticulopsocus*. Probably selection pressure leading to reticulate fore wings differs considerably in these phylogenetically very distant groups.

KEY TO GENERA OF PROTROCTOPSOCIDAE

NOTE. Figures of *Protoctopsocus* have been published by Mockford (1967, female) and Garcia Aldrete (1982, male) and additional information is given in Figs 25-30 of the present paper. For *Chelyopsocus* and *Philedaphia* see Figs 24 and 31 and figures in Lienhard (1998). The male of *Chelyopsocus* is not known. All known species of Protoctopsocidae are mentioned in the "Introduction".

- 1 Antenna 15-segmented. Head capsule clearly elongated in anterior view, frons distinctly longer than postclypeus (Garcia Aldrete, 1982: fig. 1). P4 basally enlarged, its maximal width near base (Mockford, 1967: fig. 46 and Garcia Aldrete, 1982: fig. 8). Fore femur with a longitudinal ventral row of short articulated spines on anterior side (Mockford, 1967: fig. 29; Garcia Aldrete, 1982: fig. 4). Female subgenital plate (Fig. 25) with 2-5 (usually 4)¹⁾ stout apical setae, lacking sclerotized latero-dorsal zones on margin. Phallosome (Fig. 30) V-shaped, without medio-apical sclerite, lateral struts straight, simple; endophallus lacking pore-bearing central lobe. Fore wing not sexually dimorphic, normally shaped in macropterous morph (Mockford, 1967: fig. 26), slightly elytriform with concave wing cells but with normal venation in brachypterous morph (Garcia Aldrete, 1982: fig. 2); this morph known in both sexes
 *Protoctopsocus* Mockford
- Antenna 14-segmented. Head capsule weakly elongated, nearly circular in anterior view, frons not or only slightly longer than postclypeus. P4 nearly spindle-shaped, its maximal width roughly in the middle (Fig. 20). Fore femur with a longitudinal ventral row of particularly well-developed sculptural denticles (not articulated!) on anterior side (Fig. 22). Female subgenital plate (Fig. 12) with 2 (rarely 3) stout apical setae and with sclerotized latero-dorsal zones on margin, these more or less distinctly joined to T-shaped sclerite by small sclerotized bridges. Phallosome relatively complex, with medio-apical sclerite (Lienhard, 1998: fig. 45d) or lateral struts curved inward (Figs 9, 11); endophallus with a pore-bearing central lobe (Figs 9, 11, 31). Fore wing normal (Pl. 2A) or strongly elytriform and with modified venation (Pls 1AB, 2B), sometimes sexually dimorphic 2
- 2 Incisive region of mandibles blunt (Fig. 24). Apex of outer cusp of lacinial tip broad, only with a slight marginal incision (Lienhard, 1998: fig. 43d). Brachypterous female with elytriform fore wing, venation modified to form concave "honeycombed" cells (Pl. 2B and Lienhard, 1998: fig. 43a, e; pl. 9g) *Chelyopsocus* Lienhard
- Incisive region of mandibles acute (Fig. 21). Apex of outer cusp of lacinial tip with distinct indentation (Fig. 19). Brachypterous female

¹⁾ Mockford (1967: fig. 37) illustrated a subgenital plate with only 2 stout apical setae; the specimen examined has 5 such setae (Fig. 25). In 1979 Mockford (in litt.) stated: "4 stout setae is the usual situation for both forms" [i. e. for macropterous and brachypterous morphs].

- with normally shaped fore wing and slightly reduced venation (Lienhard, 1998: fig. 46a, pl. 3a) or with reticulate elytriform fore wing (Fig. 1 and Pl. 1A) 3
- 3 Fore wing normally shaped in macropterous morph (male and female) (Pl. 2A) and in brachypterous morph (female), venation normal in both morphs but slightly reduced in brachypterous females. Phallosome U-shaped (Lienhard, 1998: fig. 45d), with medio-apical sclerite; lateral struts of phallosome doubled, not curved to the middle at their apex. Angle of lateral hind margin of clunium with a densely pilose posterior lobe (Lienhard, 1998: fig. 45a) *Philedaphia* Lienhard
- Only brachypterous morph known (male and female), fore wing elytri-form with somewhat simplified venation in male (Figs 4-6; Pl. 1B) and with reticulate venational pattern in female (Fig. 1; Pl. 1A). Phallosome V-shaped (Figs 9, 11), lacking medio-apical sclerite; lateral struts simple but curved to the middle at their apex. Lateral hind margin of clunium simple, roughly right-angled, without densely pilose posterior lobe (Fig. 8) *Reticulopsocus* gen. n.

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